

Evolving synergetic interactions

Bin Wu¹, Jordi Arranz¹, Jinming Du², Da Zhou³ and Arne Traulsen¹

¹ Department of Evolutionary Theory, Max Planck Institute for Evolutionary Biology,
August-Thienemann-Straße 2, 24306 Plön, Germany,

² Center for Systems and Control, College of Engineering, Peking University,
Beijing 100871, China

³ School of Mathematical Sciences, Xiamen University,
Xiamen 361005, China

September 10, 2015

Abstract

1
2 **The outcome of a major evolutionary transition is the aggregation of inde-**
3 **pendent entities into a new synergetic level of organisation. Classical models**
4 **involve either pairwise interactions between individuals or a linear superposi-**
5 **tion of these interactions. However, major evolutionary transitions display syn-**
6 **ergetic effects: their outcome is not just the sum of its parts. Multiplayer games**
7 **can display such synergies, as their payoff can be different from the sum of any**
8 **collection of two-player interactions. Assuming that all interactions start from**
9 **pairs, how can synergetic multiplayer games emerge from simpler pairwise in-**
10 **teraction? Here, we present a mathematical model that captures the transition**
11 **from pairwise interactions to synergetic multiplayer ones. We assume that dif-**
12 **ferent social groups have different breaking rates. We show that non-uniform**
13 **breaking rates do foster the emergence of synergy, even though individuals**
14 **always interact in pairs. Our work sheds new light on the mechanisms under-**
15 **lying a major evolutionary transition.**

16 **Keywords:** multiplayer games, synergetic interactions, evolutionary transition

17 **1 Introduction**

18 Major evolutionary transitions share cooperation as a common theme: simple units aggregate to
19 form a new level of organisation in which individuals benefit others bearing a cost to themselves
20 (1, 2). However, from a Darwinian perspective, cooperation is difficult to explain, as natural selec-
21 tion promotes selfishness rather than cooperation (3–7). The evolution of cooperation has often
22 been approached through the lens of simple two-player games that depict social dilemmas (8–
23 10). The study of games such as the Prisoner’s Dilemma, or alternative situations such as the
24 Stag-Hunt game (11), have provided insightful views on which mechanisms are likely to promote
25 cooperation — e.g., spatial reciprocity, direct reciprocity, indirect reciprocity, kin selection and
26 group selection (12–14). However, the simplicity of two-player games is a double-edged sword,
27 as these pairwise games may fail to capture the intricacies of complex interactions in real social
28 and biological systems. Evolutionary transitions typically involve multiple interaction partners at
29 the same time rather than a collection of pairwise interactions. For instance, when cells interact
30 to form a multicellular organism, a superposition of pairwise interactions is insufficient to capture
31 the intricacies of the complex organism. This is because an interaction among all the cells is not
32 just a sum of pairwise interactions. Synergetic interactions — the whole being more than the sum
33 of its parts — may be necessary to allow a high level of selection unit to emerge. Synergetic
34 interactions could then pave the way for the emergence of complex phenomena such as division
35 of labour or multicellularity. Therefore, understanding how synergetic interactions emerge is an
36 important part of our understanding of evolutionary transitions.

37 General multiplayer games, which cannot be decomposed into pairwise interactions, can rep-
38 resent such synergy effects. They can display broader and richer dynamics than their traditional
39 two-player counterparts (15–18). In particular, multiplayer games can exhibit payoff non-linearities
40 and can thus account for the synergetic effects that are intrinsic to major evolutionary transitions.
41 Although the emergence of synergetic interactions among multiple players is key to all major evo-
42 lutionary transitions as aforementioned (19), we lack fundamental understanding on how such
43 complex synergetic interactions occur in the first place. Here, we present a mathematical model
44 that captures the emergence of synergetic multiplayer games from simple pairwise interactions.

45 **2 Results**

46 **2.1 Model description**

47 We consider a structured population of N individuals, assorted into l sets (20), each consisting
48 of m individuals. Individuals can have a different number of set memberships and play one of
49 two strategies, A or B . An individual accumulates the payoff through interactions within all the
50 sets it belongs to. These interactions are always pairwise and the payoff depends on the set
51 configuration, i.e., the number of individuals playing A and B in the set. At every time-step, either
52 the strategy of an individual or the set structure is updated. With probability w , the strategy of an
53 individual is updated. Two individuals are randomly chosen and one imitates the other's strategy
54 with a probability that increases with the payoff difference. Individuals with higher payoffs are
55 more likely to be imitated (21, 22). With probability $1 - w$, a set is randomly chosen. This set may
56 break up with probability k_i — where i is the number of strategy A individuals in the set, ranging
57 from 0 to m . As a consequence, k_i determines the fragility of a set, which in turn, depends on
58 the set composition (23). If the set breaks, a randomly chosen individual — which belongs to at
59 least one other set — is expelled. In order to keep the size of the set constant, another random
60 individual is then incorporated into the set (Fig.1).

61 Although our model is simple, it captures two fundamental aspects. First, the set structure
62 mimics the social interactions which is an intrinsic characteristic of biological systems and human
63 societies. For instance, the set size could be based on the diffusion rate of the public goods se-
64 creted by cooperative cells (24, 25). The overall structure also allows to consider an organisation
65 of arbitrary size, from a small family to a large assembly. Second, individuals only interact in
66 pairs and payoffs are additive. In this case, the payoff of an individual is nothing but sum of the
67 corresponding pairwise interactions. Thus, there are no imposed synergetic effects via the payoff
68 accumulation process. Instead, it can only emerge from the dynamics of the population structure.

69 **Pairwise games between two strategies**

70 If the size of the sets is two, $m = 2$, the population structure is equivalent to a network, where
71 a “set” becomes a “link” (Fig. 1). In this case, the accumulated payoffs can still be captured by
72 a pairwise interaction, hence there is no synergetic multiplayer interactions (26, 27). Although
73 our analytical framework is general enough to allow the study of any set size, we focus on the

74 case where $m = 3$, that is, when the sets contain three individuals. Let us assume that for two
 75 individuals playing strategy A (B), each one obtains a payoff of a (d). Similarly, for two individuals
 76 playing different strategies, the individual using strategy A obtains the payoff b and the individual
 77 using strategy B obtains the payoff c . Given that there are three individuals in every set, the
 78 payoff of an individual within a set is determined by two pairwise interactions. Therefore, the
 79 payoff of an individual playing strategy A (B) in a set with j other individuals playing A is given by
 80 $a_j = aj + b(2 - j)$ ($b_j = cj + d(2 - j)$). Note that for $m = 3$, $j = 0, 1, 2$. Given that the breaking
 81 probability of a specific set may depend on the number of A individuals within the set, the set
 82 dynamics allows for non-uniform breaking probabilities across the sets.

83 To demonstrate that our simple model can indeed capture the emergence of synergy, we
 84 consider two aspects: the accumulated payoff of both types and the evolutionary dynamics of
 85 the two strategies. We find that non-uniform breaking probabilities across the sets foster the
 86 emergence of synergetic multiplayer interactions. In other words, when the fragilities of the sets
 87 are non-uniform we find that (i) the expected accumulated payoff of both strategies is consistent
 88 with the one of a typical multiplayer game that cannot be decomposed into a pairwise game, and
 89 (ii) the evolutionary dynamics of the strategies exhibit two internal equilibria of selection, which is
 90 impossible in a two-player game.

91 The calculation of the average accumulated payoff in the general case is challenging, even
 92 though the model is simple. We overcome this problem by assuming that the probability with
 93 which the strategy is updated is small, $w \ll 1$. As a consequence, the set structure can reach its
 94 stationary state — which determines the accumulated payoffs — before a strategy update occurs.
 95 Importantly, the average accumulated payoffs for both strategies are consistent with the payoffs
 96 of the following 3-player game in a well mixed population, up to a positive rescaling factor (see SI
 97 Appendix, Section 2.1):

Opposing A players	0	1	2
A	a_0/k_1	a_1/k_2	a_2/k_3
B	b_0/k_0	b_1/k_1	b_2/k_2

(1)

98 Here a_i/k_{i+1} is the payoff for an individual using strategy A when it meets i opponents using

99 strategy A . Equivalently, b_i/k_i is the payoff for an individual using strategy B when it meets i
100 opponents using strategy A . The payoff table in Eq.(1) has two important features. First, the
101 derived multiplayer game is of the same size as that of the set. Second, the payoff entries are
102 proportional to the product of the accumulated payoff in a set and its lifetime.

103 The evolutionary outcome of both strategies can be predicted by the replicator equation for
104 a large class of microscopic imitation rules, if the population size is sufficiently large (see SI
105 Appendix, Section 2.2). The replicator equation is given by

$$\dot{x}_A = x_A(1 - x_A)(f_A - f_B), \quad (2)$$

106 where

$$f_A = \sum_{s=0}^2 \frac{a_s}{k_{s+1}} \binom{2}{s} x_A^s (1 - x_A)^{2-s}, \quad [3]$$

$$f_B = \sum_{s=0}^2 \frac{b_s}{k_s} \binom{2}{s} x_A^s (1 - x_A)^{2-s} \quad [4]$$

107 are the payoffs for strategy A and B of the 3-player game based on Eq. (1), and x_A is the fraction
108 of individuals using strategy A . In other words, the dynamics of the pairwise game under active
109 set dynamics can be captured by a multiplayer game in a well-mixed population. The internal
110 equilibria of this equation are the roots of the equation $f_A - f_B = 0$. Based on the initial fraction
111 of individuals using strategy A , these equilibria determine where an infinite population would end
112 up (28).

113 The above results on the accumulated payoffs and the evolutionary dynamics of strategies
114 hold for any set fragilities (k_0, k_1, k_2, k_3) . In the following, we apply these results to homogenous
115 and heterogeneous set fragilities to address when and how synergetic interactions emerge.

116 Whenever the fragility of the sets is homogenous, $k_0 = k_1 = k_2 = k_3$, Eq. (1) is identical
117 to the one of the original pairwise game, even though it is a 3-player game (see SI Appendix,
118 Section 2.2). Therefore there is no synergy effect in the payoffs. Given that the replicator equation
119 is equivalent to the one of the pairwise game, there is at most one internal equilibrium with the
120 same position and stability. The upper panel of Fig. 2 shows the agreement between the analytical
121 approximation and a simulation of the full model.

122 However, when fragilities are not homogeneous across the sets, Eq.(1) becomes a 3-player
123 game, which cannot be decomposed into additive pairwise interactions (lower panel of Fig. 2).

124 In this case, the payoff of an individual interacting with two opponents is not equal to the sum of
125 the two pairwise interactions (Fig. 3). Consequently, the presence of non-uniform set breaking
126 probabilities generates synergetic payoffs. Synergy emerges exclusively as a result of the evolu-
127 tionary dynamics of the set structured population. In addition to this, the replicator equation has
128 two internal equilibria, which is not possible in pairwise interactions (see lower panel of Fig. 2).
129 Static random networks display similar effects (29). A necessary condition for the emergence of
130 two equilibria is that the sign of the effective payoff difference $a_i/k_{i+1} - b_i/k_i$ changes twice with
131 the increase of the number of opponents using strategy A , i (30, 31). A more detailed analysis
132 on the conditions that lead to two internal equilibria can be found in SI Appendix, Section 2.2. If
133 one of the two equilibria is stable, the other has to be unstable. Given this, our model can explain
134 both the maintenance of biodiversity and phenotypic dominance within the same framework.

135 **Pairwise games between n strategies**

136 The model can be extended to account for an arbitrary number of strategies, n , instead of only
137 two. In the pairwise interactions with n strategies or an $n \times n$ game, the non-uniform breaking
138 probabilities also generate synergetic multiplayer interactions. Although the analytical calculations
139 are more intricate due to the increased number of set configurations, we find that the payoff matrix
140 of the emergent multiplayer game is consistent with the one of an n -strategy m -player game (SI
141 Appendix, Section 3.1). Interestingly, the intuition behind these payoff entries is similar to the ones
142 of the two-strategy case, as they still represent the product of the additive payoffs via pairwise
143 interactions and the duration of that set. In addition to this, the n -strategy m -player game has, at
144 most, $(m-1)^{n-1}$ isolated internal equilibria, whereas the original $n \times n$ pairwise game has at most
145 one equilibrium (SI Appendix, Section 3.2). The dynamics in our model are thus rich enough to
146 capture complex phenomena exhibited by social and biological systems.

147 **3 Discussion**

148 Synergy refers to the idea that the whole is greater than the sum of its parts. Interestingly, synergy
149 is identical to “cooperation” in ancient Greek. Synergy can be observed in a plethora of different
150 contexts such as in genes (32), microbial populations (33), and even social and economic sys-
151 tems. From an evolutionary perspective, synergy is a cornerstone of all major evolutionary tran-

152 sitions. These evolutionary milestones involve the aggregation of simple units into a new entity
153 which becomes a higher-level Darwinian unit of selection (1). With this in mind, we present a
154 minimalistic model that shows how synergy can actually emerge. Our model allows to treat the
155 emergence of synergetic interactions from simple additive pairwise ones analytically. We assume
156 that the strategy of the individuals and the set structure evolve in time. The results prove that
157 non-uniform set breaking rates, which depend exclusively on the configuration of these sets, lead
158 to payoff non-linearities. These are consistent with the dynamics of a multiplayer game, even
159 though individuals always play a two-player game and no group selection effects are present.
160 These findings rely on two conditions: i) sets must contain more than two individuals, and ii) the
161 breaking rates must depend on the configuration of the sets and, hence be non-uniform. As a
162 consequence, our model may be useful as a starting point for the investigation of the evolution of
163 more complex phenomena, e.g., synergetic interactions within the group. It shows how the ag-
164 gregation of individuals can lead to complex interactions that cannot be disentangled into simpler
165 interactions.

166 **Methods**

167 *The Fermi updating rule.* We use the Fermi update rule, given by the following algorithm:

- 168 (i) Randomly select an individual, a^* and denote its payoff as π_{a^*} ;
- 169 (ii) Randomly select another individual, b^* , among all the individuals in the sets individual a^* is
170 in and denote the payoff of b^* as π_{b^*} ;
- 171 (iii) a^* switches to the strategy of b^* with probability $(1 + \exp[-\beta(\pi_{b^*} - \pi_{a^*})])^{-1}$.

172 *Accumulated payoffs.* Each data point is the average of 100 independent realisations. Every real-
173 isation takes 10^6 generations. In each realisation, for the first 10^4 generations, only set dynamics
174 occur. For the rest generations, at every step, with probability $w = 10^{-3}$ we compute the average
175 accumulated payoff of each strategy. Otherwise, with probability $1 - w$, set dynamics happens. At
176 the end of each realisation, we compute the mean value of all the average accumulated payoff.

177 *Selection gradient.* Each data point is the average of 100 independent realisations. Every reali-
178 sation takes 10^7 generation. For the first 10^4 generations of each realisation, only set dynamics
179 occur. After that, with a probability of $w = 10^{-3}$ two individuals are chosen randomly from the en-
180 tire population. The first individual is the “focal” one which is the one that may imitate the strategy

181 of the second one based on the Fermi rule. We keep track of the transition without implementing
182 them. We denote y and z as the number of times that an individual playing strategy A and B
183 changes its strategy. $\frac{z-y}{Q}$ is the estimator of the selection gradient x_A , where Q is the number of
184 strategy updating events in this realisation.

185 *Accumulated group payoffs.* Each data point is the average of 100 independent realisations.
186 Every realisation takes 10^6 generations. In each realisation, for the first 10^4 generations, only set
187 dynamics occur. For the rest generations, at every step, with probability $w = 10^{-3}$ we compute
188 the average accumulated payoff of each strategy induced by the set with 0, 1 and 2 strategy A
189 opponents, respectively. Otherwise, with probability $1 - w$, set dynamics happens. At the end of
190 each realisation, we compute the mean value of all the average accumulated payoff.

191 **Acknowledgements**

192 We thank Chaitanya Gokhale for inspiring discussions.

193 **References**

- 194 [1] Maynard Smith, J. and Szathmary, E. *The major transitions in evolution*. W. H. Freeman,
195 Oxford, (1995).
- 196 [2] Michod, R. E. Cooperation and conflict in the evolution of individuality. i. multilevel selection
197 of the organism. *The American Naturalist* **149**, 607–645 (1997).
- 198 [3] Darwin, C. *On the origin of species by means of natural selection*. Cambridge-London.
199 Reprinted in Harvard University Press (1964), (1859).
- 200 [4] Bonner, J. The origins of multicellularity. *Integrative Biology* **1**, 27–36 (1998).
- 201 [5] Wolpert, L. and Szathmary, E. Multicellularity: evolution and the egg. *Nature* **420**(6917),
202 745–745 (2002).
- 203 [6] Ratcliff, W. C., Denison, R. F., Borrello, M., and Travisano, M. Experimental evolution of
204 multicellularity. *Proceedings of the National Academy of Sciences USA* , 1–6 Jan (2012).
- 205 [7] Ratcliff, W. C., Fankhauser, J. D., Rogers, D. W., Greig, D., and Travisano, M. Origins of
206 multicellular evolvability in snowflake yeast. *Nature Communications* **6**, 6102 (2015).

- 207 [8] Maynard Smith, J. *Evolution and the Theory of Games*. Cambridge University Press, Cam-
208 bridge, (1982).
- 209 [9] Taylor, C. and Nowak, M. A. Transforming the dilemma. *Evolution* **61**, 2281–2292 (2007).
- 210 [10] Broom, M. and Rychtář, J. *Game-Theoretical Models in Biology*. Chapman and Hall/CRC,
211 (2013).
- 212 [11] Skyrms, B. *The Stag-Hunt Game and the Evolution of Social Structure*. Cambridge Univer-
213 sity Press, Cambridge, (2003).
- 214 [12] Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560–1563 (2006).
- 215 [13] Fletcher, J. A. and Doebeli, M. A simple and general explanation for the evolution of altruism.
216 *Proceedings of the Royal Society B* **276**, 13–19 (2009).
- 217 [14] Nowak, M. A., Tarnita, C. E., and Antal, T. Evolutionary dynamics in structured populations.
218 *Philosophical Transactions of the Royal Society B* **365**, 19–30 (2010).
- 219 [15] Hauert, C., Michor, F., Nowak, M. A., and Doebeli, M. Synergy and discounting of coopera-
220 tion in social dilemmas. *Journal of Theoretical Biology* **239**, 195–202 (2006).
- 221 [16] Pacheco, J. M., Santos, F. C., Souza, M. O., and Skyrms, B. Evolutionary dynamics of
222 collective action in n-person stag hunt dilemmas. *Proceedings of the Royal Society B* **276**,
223 315–321 (2009).
- 224 [17] Kurokawa, S. and Ihara, Y. Emergence of cooperation in public goods games. *Proceedings*
225 *of the Royal Society B* **276**, 1379–1384 (2009).
- 226 [18] Gokhale, C. S. and Traulsen, A. Evolutionary games in the multiverse. *Proceedings of the*
227 *National Academy of Sciences USA* **107**, 5500–5504 (2010).
- 228 [19] Tarnita, C. E., Taubes, C. H., and Nowak, M. A. Evolutionary construction by staying together
229 and coming together. *Journal of Theoretical Biology* **320**(0), 10–22 (2013).
- 230 [20] Tarnita, C. E., Antal, T., Ohtsuki, H., and Nowak, M. A. Evolutionary dynamics in set struc-
231 tured populations. *Proceedings of the National Academy of Sciences USA* **106**, 8601–8604
232 (2009).

- 233 [21] Blume, A. Communication, risk, and efficiency in games. *Games and Economic Behavior*
234 **22**, 171–202 (1998).
- 235 [22] Szabó, G. and Fáth, G. Evolutionary games on graphs. *Physics Reports* **446**, 97–216
236 (2007).
- 237 [23] Simon, B., Fletcher, J. A., and Doebeli, M. Towards a general theory of group selection.
238 *Evolution* **67**(6), 1561–1572 (2013).
- 239 [24] Gore, J., Youk, H., and van Oudenaarden, A. Snowdrift game dynamics and facultative
240 cheating in yeast. *Nature* **459**, 253–256 (2009).
- 241 [25] Xavier, J. B. Social interaction in synthetic and natural microbial communities. *Molecular*
242 *Systems Biology* **7**, 483 (2011).
- 243 [26] Wu, B., Zhou, F., Luo, Q., Wang, L., and Traulsen, A. Evolution of cooperation on stochastic
244 dynamical networks. *PLoS One* **5**, e11187 (2010).
- 245 [27] Pacheco, J. M., Traulsen, A., and Nowak, M. A. Coevolution of strategy and structure in
246 complex networks with dynamical linking. *Physical Review Letters* **97**, 258103 (2006).
- 247 [28] Hofbauer, J. and Sigmund, K. *Evolutionary Games and Population Dynamics*. Cambridge
248 University Press, Cambridge, UK, (1998).
- 249 [29] Pinheiro, F. L., Santos, F. C., and Pacheco, J. M. How selection pressure changes the nature
250 of social dilemmas in structured populations. *New Journal of Physics* **14**, 073035 (2012).
- 251 [30] Farouki, R. T. The bernstein polynomial basis: A centennial retrospective. *Computer Aided*
252 *Geometric Design* **29**, 379–419 (2012).
- 253 [31] Peña, J., Lehmann, L., and Nöldeke, G. Gains from switching and evolutionary stability in
254 multi-player matrix games. *Journal of Theoretical Biology* **346**, 23–33 (2014).
- 255 [32] Sanjuán, R. and Elena, S. F. Epistasis correlates to genomic complexity. *Proc Natl Acad Sci*
256 *U S A* **103**(99), 14402–14405 (2006).
- 257 [33] Chelo, I. M., Nédli, J., Gordo, I., and Teotónio, H. An experimental test on the probability of
258 extinction of new genetic variants. *Nat Commun* **4**(2417) 09 (2013).

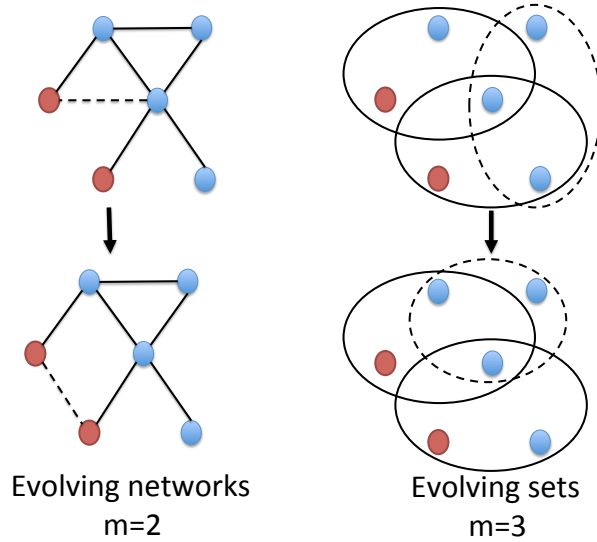


Figure 1: Set dynamics for sets of size $m = 2$ (left column) and $m = 3$ (right column). Blue and red dots represent strategies A and B respectively. When $m = 2$ (left column) “sets” are actually “links” and the overall structure is a network (26). In this case, interactions are strictly pairwise, hence there is no synergetic effect in the payoffs. The right column shows the case with $m = 3$, which is the minimum set size that illustrates the emergence of synergetic interactions. With probability $1 - w$ a set is selected at random (dashed lines). This set breaks up with probability k_i , where i is the number of strategy A individuals in the set. If the set breaks, a randomly chosen individual is expelled. In order to keep the size of the set constant, another random individual is incorporated into the updated set (dashed lines).

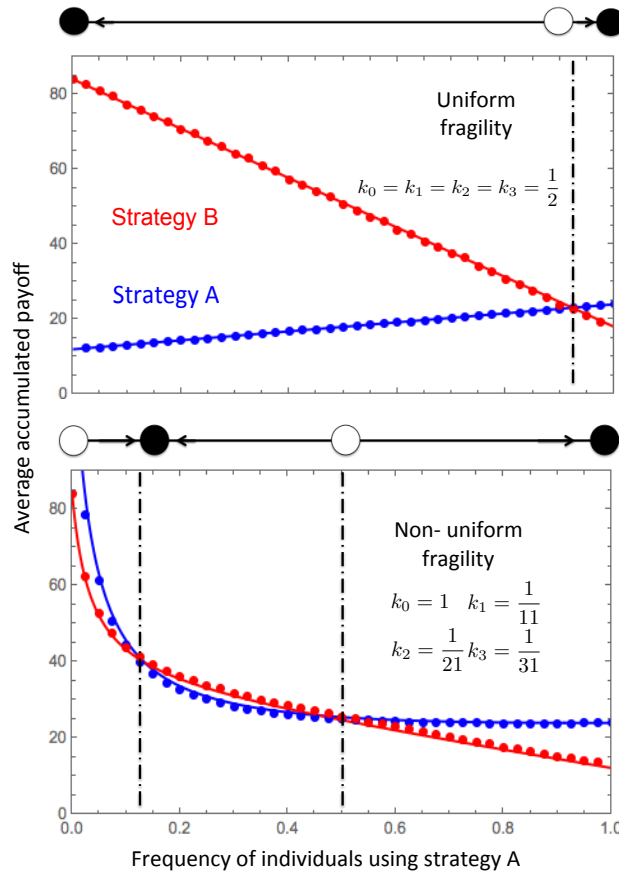


Figure 2: Accumulated payoffs for the Stag-Hunt game and the equilibria of the selection gradient for two fragility scenarios. The full/empty circles on top of each of the two panels show the analytical approximation for the stable/unstable equilibria of the replicator dynamics. Top: For uniform breaking rates, the accumulated payoffs for both strategies match the ones of a pairwise game. Thus, the payoffs change linearly with the fraction of A individuals and the replicator equation predicts just the single internal equilibrium of the pairwise game. Bottom: When the breaking rates depends on the set configuration, the payoffs for both strategies become non-linear. The more A individuals a set has, the less likely it breaks up. The payoffs for both strategies have two interSections, which lead to two internal equilibria. This illustrates that non-uniform interactions can lead to the emergence of synergetic interactions. There is a perfect agreement between simulations (dots) and analytical approximation (lines). (Parameters: Stag-Hunt game with $a = 2$, $b = 1$, $c = 1.5$ and $d = 7$. Population size, $N = 500$, number of sets, $l = 1000$, probability of a strategy update, $w = 10^{-3}$. Selection intensity, $\beta = 0.1$. See Methods for the simulation details).

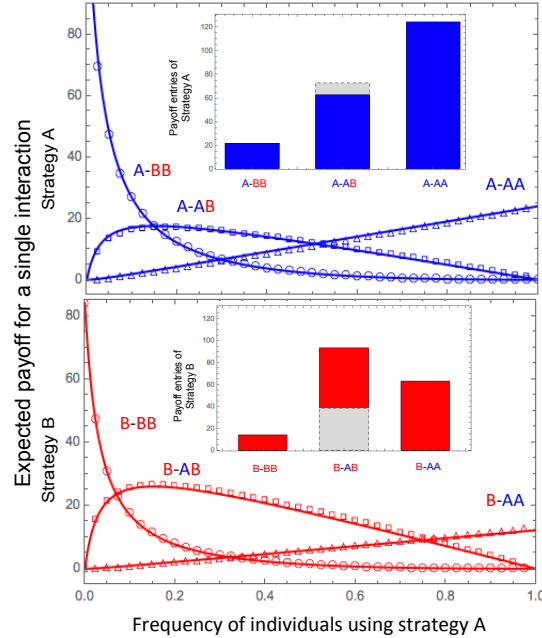


Figure 3: Expected payoffs for individuals using strategies A (upper panel) and B (lower panel) in groups of different compositions. The two insets within each plot show the effective payoff entries of the emergent 3-player game Eq. (1) for a frequency of 0.5. Main panels: Theoretical predictions for the payoff within the three set configurations of each individual, Eqs. (3) and (4) (lines) agree well the accumulated payoff obtained by simulation (symbols). This in turn proves that the synergetic 3-player game is intrinsically captured by Eqs. (3) and (4) even term by term. Upper inset: Payoffs for equal abundance of both strategies. An individual with strategy A gains less if it interacts in a set which has 1 individual with strategy A than it were in the synergy free case (grey, dashed). Lower inset: An individual with strategy B gains much more if it interacts in a set which has 1 individual with strategy A than it were in the synergy free case (grey, dashed). Here the payoffs in the synergy free cases are the average values of the two payoff entries for the focal individual interacting with 0 and 2 A individuals. Thus, the interaction can no longer be decomposed into multiple pairwise interactions, which is how every individual obtains its payoff microscopically. (Parameters are the same as that in the lower panel of Fig. 2. The inner panels are obtained by simulation via setting the frequency of individuals using strategy A to be one half. See Methods for the simulation details.)

Supplementary Information of “Evolving synergetic interactions”

Bin Wu¹, Jordi Arranz¹, Jinming Du², Da Zhou³ and Arne Traulsen¹

¹ Department of Evolutionary Theory, Max Planck Institute for Evolutionary Biology,
August-Thienemann-Straße 2, 24306 Plön, Germany,

² Center for Systems and Control, College of Engineering, Peking University,
Beijing 100871, China

³ School of Mathematical Sciences, Xiamen University,
Xiamen 361005, China

September 10, 2015

1 Contents

2	1 Evolutionary dynamics in a set structured population	2
3	2 Games with two strategies	3
4	2.1 Accumulated payoffs	3
5	2.2 Evolutionary dynamics of strategies	6
6	3 Games with n strategies	8
7	3.1 Accumulated payoffs	8
8	3.2 Evolutionary dynamics of strategies	12

9 1 Evolutionary dynamics in a set structured population

10 Consider a set structured population of fixed size N where individuals engage in a pairwise game.
11 The population is divided into a constant number of sets, l , each of them of constant size m .
12 Individuals can belong to different sets.

13 At each time step, we either update the strategy of an individual — with probability w — or the
14 structure of the population, with probability $1 - w$.

15 A strategy update involves two randomly selected individuals, say Alice and Bob. Alice imi-
16 tates Bob's strategy with a probability depending on the difference of their payoffs, i.e., the imita-
17 tion rule (1). The payoff of an individual is calculated as the sum of all the pairwise interactions
18 through all the sets it belongs to. For instance, if Alice belongs to two sets, her payoff is the sum
19 of the payoff in the first set, plus the payoff in the second one. Given that every set consists of
20 m individuals, the payoff of an individual in a set is the sum of $m - 1$ pairwise interactions. On
21 the other hand, when set dynamics occur, a set is randomly selected. This set may break with a
22 probability which depends on the set composition. In particular, if there are only two strategies,
23 the set composition is the number of individuals within the set playing a specific strategy. If the
24 set is broken, a random individual within the set is expelled, provided it is in at least one other set.
25 In order to keep the size of the set constant, another random individual is added to the focal set.

26 We start with the simplest pairwise games with two strategies, A and B . The 2×2 payoff
27 matrix is given by $(a_{ij})_{2 \times 2}$, where a_{ij} is the payoff of an individual playing strategy i with an
28 opponent playing strategy j , where $i, j \in \{A, B\}$. We find that the average accumulated payoff for
29 each strategy is consistent with the one of a 2-strategy, m -player game up to a positive rescaling
30 factor. When the breaking probability of a set is uniform across all kinds of sets, the payoff of
31 the m -player game is equivalent to that of a sum of $m - 1$ pairwise games. However, we notice
32 that whenever the sets have different breaking probabilities that depend on the set composition,
33 intrinsic multiplayer interactions emerge. In this case, the accumulated payoff of both strategies
34 cannot be decomposed into collections of pairwise games anymore. In other words, synergetic
35 effects in payoff can emerge from simple pairwise interactions. Based on accumulated payoffs,
36 we further obtain the replicator equation of the m -player game to determine the evolutionary fate
37 of each strategy. In addition to this, the replicator equation shows up to $m - 1$ internal equilibria.
38 In contrast, for pairwise interaction there is at most one such equilibrium. These results are
39 obtained under the assumption of fast set dynamics — very few strategy updates occurs before

40 the population structure has reached the stationary state — and a large population size.

41 We generalise the above results for cases where the number of strategies, n , is greater than
42 two. In this case the payoff matrix is given by $(a_{ij})_{n \times n}$, where $i, j \in \{1, 2, \dots, n\}$. In this technically
43 somewhat more challenging case, we find similar results:

44 (i) The average accumulated payoff of each strategy is of the form of an n -strategy, m -player
45 game up to a positive rescaling factor.

46 (ii) When the set breaking probabilities are uniform, the payoff of the n -strategy m -player game
47 is still consistent with the sum of the $m - 1$ pairwise games.

48 (iii) Non-uniform set breaking probabilities foster the emergence of multiplayer interactions,
49 which cannot be decomposed into a collection of pairwise games.

50 (iv) The replicator equation of the n -strategy m -player captures evolutionary dynamics of the
51 strategies and displays, at most, $(n - 1)^{m-1}$ internal equilibria, whereas pairwise $n \times n$
52 games display, at most, a single equilibrium (2).

53 2 Games with two strategies

54 2.1 Accumulated payoffs

55 Initially, i.e. at time $t = 0$, we call the l sets T_i^0 , $1 \leq i \leq l$. For the first time step in the set evolution,
56 $t = 1$, we denote the selected set as $T_{i^*}^0$. If this set is broken and transforms to another set, we
57 denote the transformed set as $T_{i^*}^1$, otherwise the set is not broken and we let $T_{i^*}^1 = T_{i^*}^0$. For the
58 other sets which are not selected, we denote $T_i^1 = T_i^0$, $i \neq i^*$. Recursively, we define T_i^t for $t \geq 0$
59 and $1 \leq i \leq l$.

60 Let $\psi(T_i^t)$ be the number of strategy A individuals in set T_i^t , thus $0 \leq \psi(T_i^t) \leq m$. For each set
61 i , the dynamics of $\psi(T_i^t)$ is a Markov chain in state space $\{0, 1, 2 \dots m\}$ with the transition matrix

$$Q = \frac{1}{l}V + \frac{l-1}{l}I_{m+1}, \quad [1]$$

62 where I_{m+1} is the identity matrix of size $m+1$ and V is the transition matrix when set i is selected.

63 Hence, $V = (V_{ij})_{(m+1) \times (m+1)}$ ($0 \leq i, j \leq m$) is a tridiagonal matrix given by

$$V_{ij} = \begin{cases} k_i \frac{m-i}{m} x_A & \text{if } j = i + 1 \\ 1 - k_i \left(\frac{m-i}{m} x_A + \frac{i}{m} x_B \right) & \text{if } j = i \\ k_i \frac{i}{m} x_B & \text{if } j = i - 1 \\ 0 & \text{otherwise} \end{cases}. \quad [2]$$

64 Here x_A and $x_B = 1 - x_A$ are the fractions of strategy A and B in the population, k_i is the
65 breaking probability of a set consisting of i individuals playing strategy A and $m - i$ individuals
66 playing strategy B .

67 When $x_A > 0$ and $x_B > 0$, the matrix Q is irreducible and aperiodic and there is a unique
68 stationary distribution $y = (y_0, y_1, \dots, y_m)$ of Q determined by $yQ = y$. Taking Eq. (1) into $yQ = y$
69 leads to $yV = y$. This leads to the stationary distribution

$$y_s = \frac{1}{\mathcal{N} k_s} \binom{m}{s} x_A^s x_B^{m-s}, \quad 0 \leq s \leq m, \quad [3]$$

70 where $\mathcal{N} = \sum_{s=0}^m \binom{m}{s} \frac{1}{k_s} x_A^s x_B^{m-s} > 0$ is a normalisation factor. The stationary distribution also
71 represents the proportion of each type of set among all the sets in the stationary regime.

72 When set dynamics are fast, the imitation event happens rarely enough to allow the population
73 structure to reach the stationary state before a single imitation event occurs. In this case, the
74 stationary regime of the set dynamics determines the average payoff of both strategies. Here the
75 accumulated payoff of strategy A is given by

$$\begin{aligned} f_A &= \frac{\text{Total payoff of all the strategy } A \text{ individuals}}{\text{Number of strategy } A \text{ individuals}} \\ &= \frac{\sum_{j=1}^m l y_j j (a_{AA}(j-1) + a_{AB}(m-j))}{\mathcal{N} x_A} \\ &= \frac{1}{\mathcal{N}} \frac{l}{N} \sum_{j=1}^m \binom{m}{j} j \frac{1}{k_j} x_A^{j-1} x_B^{m-j} \underbrace{(a_{AA}(j-1) + a_{AB}(m-j))}_{a_{j-1}}. \end{aligned} \quad [4]$$

76 As $j \binom{m}{j} = m \binom{m-1}{j-1}$, Eq. (4) can be written as

$$\frac{1}{\mathcal{N}} \frac{lm}{N} \sum_{j=1}^m \binom{m-1}{j-1} x_A^{j-1} x_B^{m-j} \frac{a_{j-1}}{k_j}. \quad [5]$$

77 With $s = j - 1$, Eq (5) becomes

$$f_A = \frac{1}{\mathcal{N}} \frac{lm}{N} \underbrace{\sum_{s=0}^{m-1} \binom{m-1}{s} x_A^s x_B^{m-1-s} \frac{a_s}{k_{s+1}}}_{\tilde{f}_A}. \quad [6]$$

78 Similarly, we have

$$f_B = \frac{1}{\mathcal{N}} \frac{lm}{N} \underbrace{\sum_{s=0}^{m-1} \binom{m-1}{s} x_A^s x_B^{m-1-s} \frac{b_s}{k_s}}_{\tilde{f}_B}, \quad [7]$$

79 where $b_s = a_{BA}s + a_{BB}(m - 1 - s)$ is the accumulated payoff of an individual using strategy B
 80 gets in a set consisting of s individuals using strategy A .

81 Besides the common positive rescaling factor $\frac{1}{\mathcal{N}} \frac{lm}{N}$, the average accumulated payoffs for both
 82 strategies are \tilde{f}_1 and \tilde{f}_2 . Interestingly \tilde{f}_A and \tilde{f}_B are exactly the payoff of an m -player game in a
 83 well-mixed population,

Opposing strategy A players	0	...	s	...	$m - 1$	
Strategy A	a_0/k_1	...	a_s/k_{s+1}	...	a_{m-1}/k_m	
Strategy B	b_0/k_0	...	b_s/k_s	...	b_{m-1}/k_{m-1}	

84 Here a_s/k_{s+1} (b_s/k_s) is the payoff of an individual using strategy A (B) obtains when it meets
 85 s strategy A opponents. This payoff table has two remarkable features: First, the number of
 86 players in the multiplayer game and the set size are equal. Second, the payoff entries of the
 87 multiplayer game are the product of the linear collective payoff via pairwise interactions in a set
 88 and the duration of the corresponding set. Taking a_0/k_1 as an example, a_0/k_1 is the payoff of an
 89 individual playing strategy A when he interacts with 0 strategy A opponents, or $m - 1$ strategy
 90 B individuals. However, within a set, the accumulated payoff of an individual playing strategy A
 91 is given by $a_0 = (m - 1)a_{12}$ and results from the $m - 1$ pairwise interactions in the set where
 92 $1/k_1$ is the duration of the set. In other words, a_0/k_1 is the accumulated payoff rescaled with the
 93 interaction time.

94 When $m = 2$, the population structure is equivalent to a network and the sets represent links.
 95 In this case, the effective payoff table in Eq. (8) is still a pairwise game. This transformation can
 96 alter the effective payoff of both strategies, however it cannot lead to synergetic effect in payoffs
 97 as there is only one pairwise interaction in the transformed table. When $m = 3$, the emergent
 98 payoff table is consistent with a 3-player game. On one hand, we can take the payoff entries as
 99 the synergetic payoff of two individuals. On the other hand, we have the additive payoffs via the
 100 two pairwise interactions in that set. A comparison between these two payoffs can facilitate us to
 101 study when “the whole is better than the sum of its parts”, i.e., the synergetic payoff is better off
 102 than that derived by two pairwise interactions.

103 When the set breaking probabilities are uniform — i.e., k_i is constant —, we find — by Eq. (6)
 104 and Eq. (7) — that the accumulated payoffs for strategy A and B are $f_A = (m-1)(a_{11}x_A + a_{12}x_B)$
 105 and $f_B = (m-1)(a_{21}x_A + a_{22}x_B)$. That is to say that the emergent payoff is equivalent to the sum
 106 of the corresponding $m - 1$ pairwise game and therefore there is no synergy. However, when the
 107 set breaking probabilities are non-uniform, intrinsic multiple player games emerge. In this case
 108 the “whole” is different from the sum of its parts.

109 2.2 Evolutionary dynamics of strategies

110 In large well mixed populations, the evolutionary dynamics of strategies based on the imitation
 111 rule can be approximated by the Langevin equation (3)

$$\begin{aligned} \dot{x}_A &= x_A(1 - x_A) (g(\beta(f_A - f_B)) - g(\beta(f_B - f_A))) \\ &\quad + \sqrt{\frac{x_A(1-x_A)(g(\beta(f_A-f_B))+g(\beta(f_B-f_A)))}{N}} \xi. \end{aligned} \quad [9]$$

112 Here ξ is the white Gaussian noise, f_A (Eq. 6) and f_B (Eq. 7) are the average accumulated
 113 payoffs for strategy A and B , respectively. In addition, g is the imitation function capturing the
 114 likelihood of the focal individual to adopt the strategy of the opponent’s and β is the selection
 115 intensity (4). Throughout, g' is positive, implying that individuals are likely to adopt the strategy of
 116 individuals with high payoffs. In particular, the Fermi update rule is an imitation update rule with
 117 the imitation function $g(x) = [1 + \exp(-x)]^{-1}$.

118 For large population size N , the stochastic term vanishes and we obtain

$$\dot{x}_A = x_A(1 - x_A) \left(g \left[\frac{1}{N} \frac{lm\beta}{N} (\tilde{f}_A - \tilde{f}_B) \right] - g \left[\frac{1}{N} \frac{lm\beta}{N} (\tilde{f}_B - \tilde{f}_A) \right] \right). \quad [10]$$

119 Note that $\frac{1}{N} \frac{lm\beta}{N}$ is always positive and $g' > 0$, the equilibria of this equation are the same as that
 120 of the following replicator equation of the multiplayer game Eq. (8) in position and stability

$$\dot{x}_A = x_A(1 - x_A)(\tilde{f}_A - \tilde{f}_B). \quad [11]$$

121 Therefore, the evolution of a pairwise game on the evolving set structured population is cap-
 122 tured by an m -player game in a well mixed population. Under uniform breaking probabilities,
 123 the replicator equation Eq. (11) is consistent with the one of the pairwise game in well-mixed
 124 population. At most one internal equilibrium can arise in this case. Under non-uniform breaking
 125 probabilities, however, Eq. (11) can exhibit up $m - 1$ internal equilibria.

126 For any set size m , the internal roots of the replicator equation are determined by the roots of
 127 the following Bernstein polynomial (5)

$$\tilde{f}_A - \tilde{f}_B = \sum_{s=0}^{m-1} \underbrace{\left(\frac{a_s}{k_{s+1}} - \frac{b_s}{k_s} \right)}_{\Delta d_s} \binom{m-1}{s} x^s (1-x)^{m-1-s} = 0, \quad [12]$$

128 where $x \in (0, 1)$. By the variation diminishing property (6) we know that the number of the internal
 129 roots is equal to the number of sign changes of $(\Delta d_0, \Delta d_1 \dots, \Delta d_{m-1})$, or less by an even number.
 130 In particular, when there is only one sign change in the sequence $(\Delta d_0, \Delta d_1 \dots, \Delta d_{m-1})$, there
 131 is exactly one internal equilibrium.

132 When the set size m is 3, there can be, at most, two internal equilibria (Fig. 1). A necessary
 133 condition for the existence of two equilibria is either $\Delta d_0 > 0$ $\Delta d_1 < 0$ and $\Delta d_2 > 0$, or $\Delta d_0 < 0$
 134 $\Delta d_1 > 0$ and $\Delta d_2 < 0$. In both cases, the sign of the coefficient changes twice. The variation
 135 diminishing property tells us that there can be either two or no internal equilibria. Since $\Delta d_0 > 0$
 136 $\Delta d_1 < 0$ and $\Delta d_2 > 0$ is equivalent to $\Delta d_0 < 0$ $\Delta d_1 > 0$ and $\Delta d_2 < 0$ by exchanging the name
 137 of the two strategies. We focus on $\Delta d_0 < 0$ $\Delta d_1 > 0$ and $\Delta d_2 < 0$. In this case, the Bernstein
 138 polynomial Eq. (12) is negative at $x = 0$ and 1. Thus, the existence of two internal equilibria
 139 is equivalent to that the maximum of the Bernstein polynomial in $(0, 1)$ has to be positive. In the
 140 present case, the Bernstein polynomial is quadratic with a maximum at $x^* = (\Delta d_1 - \Delta d_2) / ((\Delta d_1 -$

141 $\Delta d_2) + (\Delta d_1 - \Delta d_0) \in (0, 1)$. Therefore, the Bernstein polynomial is positive at x^* if

$$-2\Delta d_0\Delta d_1\Delta d_2 + 2(\Delta d_1)^3 - \Delta d_0(\Delta d_1)^2 - \Delta d_2(\Delta d_1)^2 + \Delta d_0(\Delta d_2)^2 + \Delta d_2(\Delta d_0)^2 > 0 \quad [13]$$

142 To sum up, there are two internal equilibria if and only if either of the two conditions holds

$$\Delta d_0 < 0$$

$$\Delta d_1 > 0$$

$$\Delta d_2 < 0$$

$$-2\Delta d_0\Delta d_1\Delta d_2 + 2(\Delta d_1)^3 - \Delta d_0(\Delta d_1)^2 - \Delta d_2(\Delta d_1)^2 + \Delta d_0(\Delta d_2)^2 + \Delta d_2(\Delta d_0)^2 > 0$$

143 or

$$\Delta d_0 > 0$$

$$\Delta d_1 < 0$$

$$\Delta d_2 > 0$$

$$-2\Delta d_0\Delta d_1\Delta d_2 + 2(\Delta d_1)^3 - \Delta d_0(\Delta d_1)^2 - \Delta d_2(\Delta d_1)^2 + \Delta d_0(\Delta d_2)^2 + \Delta d_2(\Delta d_0)^2 < 0$$

144 **3 Games with n strategies**

145 In the above section we assumed that each individual plays a pairwise game with its opponent.

146 In addition, every individual can choose only between 2 strategies. In this section, we allow

147 individuals to choose any number of strategies and thus generalise our analysis to n strategies.

148 In this case, the pairwise interaction becomes an $n \times n$ game. We show that the previous results

149 also hold for n strategies when the set dynamics are fast enough as, (i) the accumulated payoff for

150 any strategy is an m -player game and (ii) the evolutionary dynamics of strategies can be captured

151 by the replicator equation of the n -strategy m -player game.

152 **3.1 Accumulated payoffs**

153 Similar to the 2-strategy case, the breaking probability of a set depends exclusively on its strategy

154 composition. Let us denote $k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}$ as the breaking probability of a set where α_s is the

155 number of strategy- s individuals in the focal set and $\alpha_s \geq 0$ and $\sum_{s=1}^n \alpha_s = m$ indicates that the
 156 set consists exactly of m individuals.

157 We start by randomly choosing one of the l sets, namely i . Then we define a sequence of
 158 sets T_i^t ($t \geq 0$). Here the set T_i^t evolves into T_i^{t+1} . The type of the set T_i^t — i.e., $\psi(T_i^t)$ — is a
 159 Markov chain whose states are given by the possible set configurations. These set configurations
 160 can be denoted as the simplex

$$S_{n,m} = \{(\alpha_1, \alpha_2 \cdots, \alpha_n) | \alpha_s \geq 0 \text{ and } \sum_{s=1}^n \alpha_s = m\}, \quad [14]$$

161 where α_s is the number of strategy s individuals in the corresponding set. The transition matrix of
 162 this Markov chain is given by

$$Q = \frac{1}{l}V + \frac{l-1}{l}I, \quad [15]$$

163 where I is the identity matrix of size $|S_{n,m}|$. Here $|S_{n,m}|$ is the cardinal number of set $S_{n,m}$. V
 164 is the transition matrix conditioned on the fact that the set i is selected. By the updating rule of
 165 the sets, two subsequent sets T_i^t and T_i^{t+1} have at least $m - 1$ individuals in common. Thus the
 166 transition is impossible between two states $(\alpha_1, \alpha_2 \cdots, \alpha_n)$ and $(\alpha'_1, \alpha'_2 \cdots, \alpha'_n)$, unless either of
 167 the following two cases holds.

- 168 • There exist two different strategies s_1 and s_2 such that $\alpha'_{s_2} = \alpha_{s_2} + 1$ and $\alpha'_{s_1} = \alpha_{s_1} - 1$; for
 169 all the other strategies s , $\alpha'_s = \alpha_s$.
- 170 • For all $1 \leq s \leq n$, $\alpha'_s = \alpha_s$.

171 In the first case, the selected set is broken; one individual playing strategy s_1 is expelled and
 172 one individual with strategy s_2 is incorporated to the set. In order to illustrate this case, we take
 173 the transition from $(\alpha_1, \alpha_2 \cdots, \alpha_n)$ to $(\alpha_1 + 1, \alpha_2 \cdots, \alpha_n - 1)$ as an example. First, a set consisting
 174 of α_s strategy s individuals is selected, and then breaks with probability $k_{(\alpha_1, \alpha_2 \cdots, \alpha_n)}$. Second, a
 175 strategy n individual is expelled (with probability α_n/m). Finally, a strategy 1 individual is incor-
 176 porated (with probability x_A , i.e., the fraction of strategy 1 in the population). Thus the transition
 177 probability is $\alpha_n x_A k_{(\alpha_1, \alpha_2 \cdots, \alpha_n)}/m$. Similarly, the transition probability from state $(\alpha_1, \alpha_2 \cdots, \alpha_n)$

178 to $(\alpha'_1, \alpha'_2, \dots, \alpha'_n)$, where the two states fulfill the first constraint, is given by

$$\frac{\alpha_{s_1}}{m} x_{s_2} k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}. \quad [16]$$

179 The second case reveals that the two subsequent states are equivalent. Either the selected
 180 set is not broken or it is broken but the expelled individual and the new individual are the same in
 181 type. In this case, the transition probability can be obtained by the normalisation property of V —
 182 i.e., one minus the sum of all the other transition probabilities in Eq. (16).

183 When all the strategies coexist, i.e., $\prod_{i=1}^n x_i \neq 0$, the transition matrix Q is aperiodic and
 184 irreducible, consequently the Markov chain presents a unique stationary distribution. By Eq. (15),
 185 the stationary distribution of Q is the same as that of V . This holds for any number of total links
 186 l . However, the size of the state space $|S_{n,m}|$ is $\binom{n+m-1}{m}$ (7). As a consequence, the number
 187 of states increases much more rapidly with the set size when there are more than two types of
 188 strategies in the population (Fig (2)). Given this, it becomes challenging to calculate the stationary
 189 distribution for multiple strategies. Still, as shown in (8), for general $n \times n$ games and the dynamical
 190 network $m = 2$, we have i) that the stationary distribution is a binomial distribution weighted by the
 191 duration time, ii) that the conditional transition matrix V satisfies the detailed balance condition.
 192 This binomial distribution arises from the network structure, which is a special case, $m = 2$, of our
 193 set structure. It turns out that these results can be generalised for $m \geq 2$.

- 194 • The stationary distribution of V , y , is a multinomial distribution weighted by the duration
 195 time, i.e.,

$$y_{(\alpha_1, \alpha_2, \dots, \alpha_n)} = \frac{1}{\mathcal{N}} \frac{m!}{\alpha_1! \alpha_2! \dots \alpha_n!} \frac{1}{k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}} \prod_{i=1}^n x_i^{\alpha_i}, \quad (\alpha_1, \alpha_2, \dots, \alpha_n) \in S_{n,m} \quad [17]$$

196 where $\mathcal{N} = \sum_{(\alpha_1, \alpha_2, \dots, \alpha_n) \in S_{n,m}} \frac{m!}{\alpha_1! \alpha_2! \dots \alpha_n!} \frac{1}{k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}} \prod_{i=1}^n x_i^{\alpha_i}$ is a normalisation factor.

- 197 • The Markov chain V fulfills the detailed balance condition, i.e.,

$$y_{(\alpha_1, \alpha_2, \dots, \alpha_n)} V_{((\alpha_1, \alpha_2, \dots, \alpha_n), (\alpha'_1, \alpha'_2, \dots, \alpha'_n))} = y_{(\alpha'_1, \alpha'_2, \dots, \alpha'_n)} V_{((\alpha'_1, \alpha'_2, \dots, \alpha'_n), (\alpha_1, \alpha_2, \dots, \alpha_n))}. \quad [18]$$

198 We prove that the distribution Eq. (17) satisfies the detailed balance condition.

199 If the transition from state $(\alpha_1, \alpha_2, \dots, \alpha_n)$ to state $(\alpha'_1, \alpha'_2, \dots, \alpha'_n)$ is impossible, then the
 200 reverse transition is also impossible. Thus, Eq. (18) holds. In the other cases, the transition is

201 possible. Therefore, the two states $(\alpha_1, \alpha_2, \dots, \alpha_n)$ and $(\alpha'_1, \alpha'_2, \dots, \alpha'_n)$ must satisfy one of the
 202 two constraints of the transition matrix.

203 If they fulfill the first constraint, i.e., there exist two different strategies s_1 and s_2 such that
 204 $\alpha'_{s_2} = \alpha_{s_2} + 1$ and $\alpha'_{s_1} = \alpha_{s_1} - 1$; for all the other strategies s , $\alpha'_s = \alpha_s$. By Eqs. (16) and (17) we
 205 have that

$$\begin{aligned}
 y_{(\alpha_1, \alpha_2, \dots, \alpha_n)} V_{((\alpha_1, \alpha_2, \dots, \alpha_n), (\alpha'_1, \alpha'_2, \dots, \alpha'_n))} &= \frac{1}{\mathcal{N}} \frac{m!}{\alpha_1! \alpha_2! \dots \alpha_n!} \frac{1}{k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}} \prod_{i=1}^n x_i^{\alpha_i} \times \frac{\alpha_{s_1} x_{s_2} k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}}{m} \\
 &= \frac{1}{\mathcal{N}} \frac{(m-1)!}{\alpha_1! \dots (\alpha_{s_1}-1)! \dots \alpha_{s_2}! \dots \alpha_n!} \prod_{i \notin \{s_1, s_2\}} x_i^{\alpha_i} \times x_{s_1}^{\alpha_{s_1}} x_{s_2}^{\alpha_{s_2}+1} \\
 &= \frac{1}{\mathcal{N}} \frac{(m-1)!}{\alpha'_1! \dots \alpha'_{s_1}! \dots (\alpha'_{s_2}-1)! \dots \alpha'_n!} \prod_{i \notin \{s_1, s_2\}} x_i^{\alpha'_i} \times x_{s_1}^{\alpha'_{s_1}-1} x_{s_2}^{\alpha'_{s_2}} \\
 &= \frac{1}{\mathcal{N}} \frac{m!}{\alpha'_1! \alpha'_2! \dots \alpha'_n!} \frac{1}{k_{(\alpha'_1, \alpha'_2, \dots, \alpha'_n)}} \prod_{i=1}^n x_i^{\alpha'_i} \times \frac{\alpha'_{s_2} x_{s_1} k_{(\alpha'_1, \alpha'_2, \dots, \alpha'_n)}}{m} \\
 &= y_{(\alpha'_1, \alpha'_2, \dots, \alpha'_n)} V_{((\alpha'_1, \alpha'_2, \dots, \alpha'_n), (\alpha_1, \alpha_2, \dots, \alpha_n))}. \quad [19]
 \end{aligned}$$

206 If they fulfill the second constraint, i.e., the two states are the same, then Eq. (18) holds
 207 naturally. Therefore the stationary distribution of Q is the multinomial distribution weighted by the
 208 duration time. Furthermore, Q fulfills the detailed balance condition.

When set dynamics are fast, the average payoff is determined by the stationary distribution of each set configuration. For any strategy $1 \leq i \leq n$, we have

$$\begin{aligned}
 f_i &= \frac{\text{Total payoff of strategy } i}{\text{Total number of strategy } i} \\
 &= \frac{\sum_{\alpha \in S_{n,m}} (ly_{\alpha}) \left[\alpha_i \left(\sum_{j=1}^n a_{ij} (\alpha_j - \delta_{ij}) \right) \right]}{N x_i}, \quad (20)
 \end{aligned}$$

209 where δ_{ij} is the Kronecker-delta and N is the population size.

210 Taking Eq. (17) into Eq. (20) leads to

$$f_i = \frac{1}{\mathcal{N}} \frac{l}{N} \sum_{(\alpha_1, \alpha_2, \dots, \alpha_n) \in S_{n,m}} \frac{m!}{\alpha_1! \alpha_2! \dots \alpha_n!} \frac{1}{k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}} x_i^{\alpha_i-1} \prod_{k \neq i} x_k^{\alpha_k} \left[\alpha_i \left(\sum_{j=1}^n a_{ij} (\alpha_j - \delta_{ij}) \right) \right] [21]$$

211 Considering that $\frac{m!}{\alpha_1! \dots \alpha_i! \dots \alpha_n!} \alpha_i = m \frac{(m-1)!}{\alpha_1! \dots (\alpha_i-1)! \dots \alpha_n!}$ yields that

$$f_i = \frac{1}{\mathcal{N}} \frac{lm}{N} \sum_{(\alpha_1, \alpha_2, \dots, \alpha_n) \in S_{n,m}} \frac{(m-1)!}{\alpha_1! \dots (\alpha_i-1)! \dots \alpha_n!} x_i^{\alpha_i-1} \prod_{k \neq i} x_k^{\alpha_k} \frac{1}{k_{(\alpha_1, \alpha_2, \dots, \alpha_n)}} \times \left(\sum_{j=1}^n a_{ij} (\alpha_j - \delta_{ij}) \right) [22]$$

212 Let $\tilde{\alpha}_k = \alpha_k - \delta_{ik}$, $(\tilde{\alpha}_1, \tilde{\alpha}_2, \dots, \tilde{\alpha}_n)$ be the co-player configuration of a strategy i individual in a set

213 $(\alpha_1, \alpha_2, \dots, \alpha_n)$. Eq. (22) is given by

$$f_i = \frac{1}{N} \frac{lm}{N} \sum_{(\tilde{\alpha}_1, \tilde{\alpha}_2, \dots, \tilde{\alpha}_n) \in S_{n, m-1}} \underbrace{\frac{(m-1)!}{\tilde{\alpha}_1! \dots \tilde{\alpha}_i! \dots \tilde{\alpha}_n! \prod_{k=1}^n x_k^{\tilde{\alpha}_k}}}_{\text{multinomial sampling}} \underbrace{\frac{1}{k(\tilde{\alpha}_1, \dots, \tilde{\alpha}_i+1, \dots, \tilde{\alpha}_n)}}_{\text{duration time} \times \text{collective payoff in the set}} \times \left(\sum_{j=1}^n a_{ij} \tilde{\alpha}_j \right) \quad [23]$$

214 This accumulated payoff is formally equivalent to an n -strategy m -player game up to a rescaling
 215 factor $\frac{1}{N} \frac{lm}{N}$. The first term is a multinomial distribution which indicates that $m - 1$ co-players are
 216 sampled randomly as if in a well-mixed population. The second term shows that the payoff of
 217 strategy i of the multi-player game is the collective payoff of strategy i in a set times the average
 218 duration time of the corresponding set. This term is dependent on (i) the pairwise interaction
 219 between strategy i and (ii) the set duration time. This explicitly generates an n -strategy m -player
 220 game from a pairwise $n \times n$ game (a_{ij}) .

221 3.2 Evolutionary dynamics of strategies

222 During the imitation process, the role model and the focal individual are both chosen randomly
 223 through the entire population. The evolution of strategies can also be approximated by the
 224 Langevin Equation. More precisely, in this case when the population is large enough, the de-
 225 mographic noise induced by the finite population size can be neglected (9). This results in the
 226 following replicator equation:

$$\dot{x}_i = x_i(f_i - \bar{f}), \quad [24]$$

227 where f_i is given by Eq. (23) and $\bar{f} = \sum_i^n x_i f_i$ is the average payoff. Consequently, the replicator
 228 equation is consistent with an n -strategy m -player game and can exhibit up to $(n - 1)^{m-1}$ internal
 229 isolated equilibria (2).

230 References

- 231 [1] Blume, A. Communication, risk, and efficiency in games. *Games and Economic Behavior* **22**,
 232 171–202 (1998).

- 233 [2] Gokhale, C. S. and Traulsen, A. Evolutionary games in the multiverse. *Proceedings of the*
234 *National Academy of Sciences USA* **107**, 5500–5504 (2010).
- 235 [3] Traulsen, A., Pacheco, J. M., and Imhof, L. A. Stochasticity and evolutionary stability. *Physical*
236 *Review E* **74**, 021905 (2006).
- 237 [4] Wu, B., Altrock, P. M., Wang, L., and Traulsen, A. Universality of weak selection. *Physical*
238 *Review E* **82**, 046106 (2010).
- 239 [5] Farouki, R. T. The bernstein polynomial basis: A centennial retrospective. *Computer Aided*
240 *Geometric Design* **29**, 379–419 (2012).
- 241 [6] Peña, J., Lehmann, L., and Nöldeke, G. Gains from switching and evolutionary stability in
242 multi-player matrix games. *Journal of Theoretical Biology* **346**, 23–33 (2014).
- 243 [7] Reingold, E. M., Nievergelt, J., and Deo, N. *Combinatorial algorithms: theory and practice*.
244 Englewood Cliffs, N.J. : Prentice-Hall, cop., (1977).
- 245 [8] Wu, B., Zhou, D., and Wang, L. Evolutionary dynamics on stochastic evolving networks for
246 multiple-strategy games. *Physical Review E* **84**(046111) (2011).
- 247 [9] Traulsen, A., Claussen, J. C., and Hauert, C. Coevolutionary dynamics: From finite to infinite
248 populations. *Physical Review Letters* **95**, 238701 (2005).

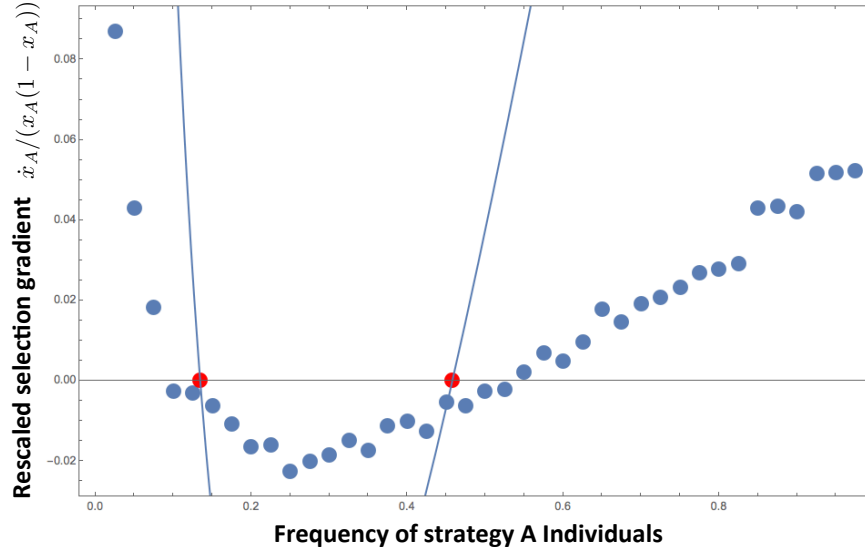


Figure 1: Rescaled selection gradient $\dot{x}_1/(x_A(1-x_A))$. The simulation based on the Fermi update rule (dots) shows that it has two roots. The analytical approximation (Eq.(10)) captures the equilibria of the selection gradient by simulation $x_A^* \approx 0.13$ and 0.46 (red dots). The absolute value of the selection gradient, however, is systematically overestimated by the theoretical approximation for the positive selection gradient. This is because there is a heterogeneity in payoffs within the population using the same strategy. Let us assume that $Q(f_A^*, f_B^*)$ is the probability that a strategy A individual is of payoff f_A^* and a strategy B individual is of payoff f_B^* . Then the selection gradient based on simulation is an estimator of $\sum_{f_A^*, f_B^*} \tanh(\frac{\beta}{2}(f_A^* - f_B^*))Q(f_A^*, f_B^*)$. Since $\tanh(x)$ is convex for $x > 0$, thus the theoretical approximation $\tanh(\frac{\beta}{2}(f_A - f_B)) = \tanh(\sum_{f_1^*, f_2^*} \frac{\beta}{2}(f_1^* - f_2^*)Q(f_1^*, f_2^*))$ is greater than the estimator of the simulation $\sum_{f_A^*, f_B^*} \tanh(\frac{\beta}{2}(f_A^* - f_B^*))Q(f_A^*, f_B^*)$. By similar arguments, we obtain that the theoretical approximation underestimates the simulation result for negative selection gradient. Each blue dot in the plot is the average of 100 independent realisations. Every realisation takes 10^7 generation. For the first 10^4 generations of each realisation, only set dynamics occur. After that, with a probability of $w = 10^{-3}$ two individuals are chosen randomly from the entire population. We keep track of the transition without implementing them. We denote y and z as the number of times that an individual playing strategy A and B changes its strategy. $\frac{z-y}{Q}$ is the estimator of the selection gradient x_A , where Q is the number of strategy updating events in this realisation. (Parameters: Stag-Hunt game with $a_{AA} = 2$, $a_{AB} = 1$, $a_{BA} = 1.5$ and $a_{BB} = 7$. Population size, $N = 500$, number of sets, $l = 1000$, probability of a strategy update, $w = 10^{-3}$. Selection intensity, $\beta = 0.1$. The breaking probabilities are $k_i = (1 + 10i)^{-1}$, where i is the number of strategy A individuals in the set.)

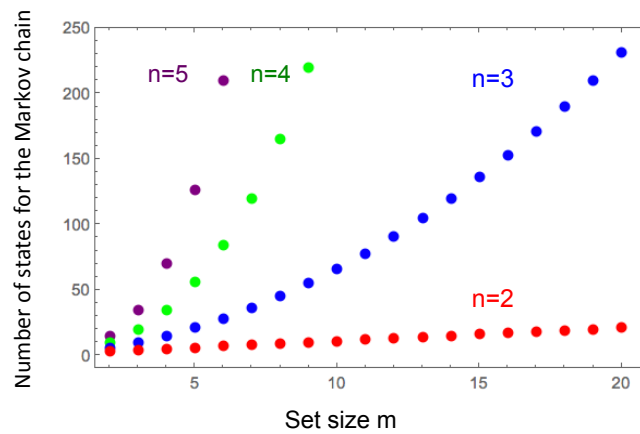


Figure 2: The size of the state space of the Markov chain of the set dynamics as a function of the set size m . For a two-strategy game, there are $m + 1$ set configurations. For a three-strategy game, there are $\binom{m+2}{2} = \frac{(m+2)(m+1)}{2}$ set configurations. In general, the number of the states increases rapidly with the size of the set, if the strategy number increases.